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Translocation of species, climate change, and the end of trying to recreate past ecological communities

Chris D Thomas

Department of Biology, University of York, York, UK, YO10 5YW

Many of the species at greatest risk of extinction from anthropogenic climate change are narrow endemics that face insurmountable dispersal barriers. In this review, I argue that the only viable option to maintain populations of these species in the wild is to translocate them to other locations where the climate is suitable. Risks of extinction to native species in destination areas are small, provided that translocations take place within the same broad geographic region and that the destinations lack local endemics. Biological communities in these areas are in the process of receiving many hundreds of other immigrant species as a result of climate change; ensuring that some of the 'new' inhabitants are climate-endangered species could reduce the net rate of extinction.

Climate change and the threat to species

Species from a variety of taxonomic groups are already shifting their distributions towards higher latitudes and elevations, as the climate warms [1–5]. However, some species disperse slowly, and many are not able to cross natural and human-created barriers [6]. Hence, distribution changes are already lagging behind the climate [7]. Species that are endemic to the summits of single mountain ranges, for example, face apparently insurmountable barriers to dispersal and a shrinking area suitable for their survival [8–10]. Many such species are projected to become extinct [8,11–16]. Comparisons of full-dispersal scenarios in which it is assumed that species are able to reach suitable climatic conditions beyond their current distributions, and no dispersal scenarios in which it is assumed that they can only survive within their existing distributions, suggest complete dispersal failure would approximately double the number of species that become extinct as a result of climate change [11]. Some of the species whose climate space has been projected to disappear entirely might still be able survive if suitable conditions exist outside the region modelled, but only if they could disperse that far. Thus, increasing the dispersal capacity of endangered species might represent the most effective climate change adaptation strategy available to conservationists who wish to reduce extinction rates.

The general principles of *in situ* and *ex situ* conservation that were developed in a 'pre-climate change' context continue to hold, and remain essential to protect biodiversity. Large quantities of high-quality habitats are still required within all biogeographic regions and centres of endemism [17]. Survival might also be enhanced by increasing habitat connectivity [18]; species require a series of stepping stones of high-quality breeding habitats to undertake multi-generational range shifts [17]. Vital as these strategies remain, a substantial proportion of the species threatened with extinction from climate change, such as single-lake endemics, species endemic to an isolated mountain range, or species that are confined to a single geological outcrop, are surrounded by environments that are fundamentally unsuitable for them. They cannot be saved by 'connecting up' the landscape between their existing distributions and potential habitats elsewhere. More widespread species might also face insurmountable barriers, such as the wrong type of geology or water, with no guarantee that they will colonise their potential destinations before existing populations dwindle to extinction.

Translocating species (i.e. assisted colonisation or assisted migration) beyond their recorded native ranges is an option when traditional strategies are insufficient [19–22]. However, the fear is that translocated species could become 'invasive' in their new ranges [23], making it essential to identify the circumstances under which the benefits of translocation outweigh the potential costs [21]. The question is whether such judgements are too difficult and the risks too high [23]; I argue here that the associated risks are predictably low in some specific situations.

In what follows, I assume that humanity wishes to minimise the number of species that will become extinct from all causes, including climate change and species invasions. Second, I assume that increased local and regional species richness is regarded as positive, provided that this does not result in higher global extinction rates. The goods and services that ecosystems provide are beyond the scope of this article, although services might often increase with increased species richness, in regions that receive translocated species.

The end of trying to recreate the past

The argument that translocations will create 'unnatural' communities is not particularly relevant in the world today. A philosophy of conserving the composition of biological communities as they are, or restoring them to some specified (or imagined) historical state, sits uneasily with

Corresponding author: Thomas, C.D. (Chris.Thomas@york.ac.uk).

 0169-5347/$ – see front matter doi:10.1016/j.tree.2011.02.006 Trends in Ecology and Evolution, May 2011, Vol. 26, No. 5

the reality of environmental and biological change. The loss of large, extinct herbivores and carnivores (megafauna) continues to affect the vegetation in remote and apparently natural areas [24–26]. Regional warming has driven species to higher elevations, even in 'undisturbed' protected areas [10,27,28], and coral reefs within marine protected areas are not immune from temperature-induced bleaching or ocean acidification [15,29]. The transport of species between continents has altered biological communities permanently, especially in the context of climate change, in otherwise undisturbed and protected areas [30–32]. Safeguarding relatively wild and remote areas remains vital, but the biota therein has already changed, and will continue to do so even under strict protection.

In more heavily transformed and disturbed regions, conservation goals often shift towards maintaining or restoring biodiversity in 'semi-natural habitats' and 'cultural landscapes' [33–35]. Traditional land management, such as hunters using fire, herders grazing domestic livestock, or woodsmen cutting trees on a rotational basis, has been carried out for hundreds or even thousands of years, but has largely been abandoned where these activities are no longer economic. Conservationists and governments replicate these activities, directly and through subsidies, to maintain traditional habitats and the rich biodiversity associated with them [33–36]. This can be important in regions where some of the species are entirely reliant on anthropogenic habitats, their original pristine habitats having long since been destroyed. However, as species change their distributions and abundances with the climate, the historic management of a particular region will no longer deliver the historic community composition. One cannot restore the historical biota associated with traditional management, in a given locality.

The changes are substantial. Recently observed rates of change in the distributions of species are sufficiently high [37] to bring about distributional changes of similar magnitude to the major distribution and community changes of the past, with novel biological associations emerging under different climatic conditions [38]. Time delays between the onset of environmental change and the stabilisation of novel communities are apparent for range changes during the past 40 years [7] and over thousands of years for responses to Holocene warming [39]. Rapid climate change sets up disequilibria between distributions and climate that might take centuries or millennia to stabilise; hence, dynamic changes to the distributions of species are already inevitable for a substantial period, even if there were to be no further warming (unrealistic as that is).

Conservation under current circumstances is about managing change; retaining or restoring past community composition is no longer feasible. Each nation or region should ask 'how can we maximise our contributions to global conservation within our region?' and avoid the unproductive 'how can we keep things as they are?'

Translocations outside the 'native ranges' of species

Translocating threatened species beyond their known native range is one means available to manage change [19–22]. Guidelines on releases into the wild for the purposes of conservation have generally only condoned the release of a species into an area where it used to occur (i.e. re-introduction, not introduction); aiming to facilitate the recovery of a species within its native range and/or restoring the ecological community [40,41]. The native range of a species is 'an area in which it was indigenous before extermination by human activities or natural catastrophe' [41]. The timescale over which the 'indigenous' or 'native' range is determined is not defined rigorously, but for most species represents records from the past few hundred (rarely few thousand) years. These guidelines were sensible in the context within which they were developed, and are in the process of being reconsidered in the context of climate change (S. Dalrymple and W. Foden, personal communication).

Existing practice already accommodates some translocation outside the known native range. Re-introductions often use genotypes from different regions if all local populations have either been extirpated or are highly inbred. The next step is to replace an extinct species with an ecologically equivalent one, aiming to restore biological communities. For example, non-native tortoises are being introduced experimentally to Round Island in the Indian Ocean, as the ecological equivalent of the extinct native tortoises [42]. Such introductions could be desirable if the translocated species are themselves endangered elsewhere, if they modify the biological community in such a way that they reduce the rate of extinction of native species in the recipient ecosystems, if they improve ecosystem services, or if they reduce the costs of ongoing management.

Scientists and conservation agencies in New Zealand have developed a successful strategy of establishing endangered species on offshore islands (where rats and other invasive species either did not colonise or have since been eliminated) regardless of whether the threatened species has ever been recorded from that specific island [43,44]. It is accepted that the benefits outweigh any negative consequences: the translocated species are endangered and the recipient community is similar to ones where the species used to occur, so major damage is unlikely. In some cases, it can be argued that the translocated species might once have occurred there naturally. Better to maintain such species somewhere in the wild, rather than condemn them to *ex situ* conservation or extinction.

The increasing climatic mismatch between the locations in which genotypes and species were naturally found and their 'ideal' environments removes part of the traditional logic of re-introducing organisms only to the locations from which they originated [22]. Re-introduction projects where the climate has deteriorated within the former distribution might now be a waste of time, but new opportunities will arise in parts of the former distribution where the climate is 'improving' for the target species [45]. This is simply incorporating climate change within the current framework. It is a small step then to introduce a species to an area 'just outside' its former distribution, translocating a species to slightly higher latitudes or elevations. For example, it might be cheaper and more practical to move species than to create extensive ecological corridors across intensively farmed land or where the intervening land has the wrong type of geology [46]. Complete transplantation

might be required, however, when the former range becomes fundamentally unsuitable. The Georgia Plant Conservation Alliance (http://www.uga.edu/gpca/project1.html) and Torreya Guardians (http://www.torreyaguardians.org/) are engaged in trying to establish the Florida-endemic *Torreya taxifolia* in the Appalachians to safeguard this ancient and Critically Endangered tree from fungal pathogens in its native range and, ultimately, from climate change. Attempts are also underway to establish a new breeding population of Endangered Bermuda petrels *Pterodroma cahow* in an area where hurricanes and sea-level rise pose less risk than in their current low-lying breeding areas [47].

Whatever conservationists do, others will continue to move genotypes and species for forestry, horticulture, agriculture, the pet trade and biomedical purposes, and accidental transport will also take place. These processes are likely to result in already widespread (largely through accidental transport) and distant species (e.g. through horticulture) having a huge dispersal advantage compared with localised species, as biological communities respond to climate change. Natural dispersal also favours already-widespread and abundant species. The 'do nothing' decision (i.e. do not translocate species deliberately) stacks the cards in favour of these types of species. Biological communities will contain hundreds or thousands of previously non-indigenous species as a result of the ongoing impacts of climate change and these other translocations. Why should they not also contain species that would otherwise be endangered?

Relict distributions and new opportunities

Narrowly distributed species that could thrive elsewhere are among the most important potential targets for assisted colonisation. These species are thought to be at greatest risk from climate change because they have small distributions, often occupy climatic conditions that are projected to disappear within the current range of the species, and are surrounded by inhospitable conditions that they are unable to cross [6,8,10,48]. If suitable climatic conditions already exist or emerge elsewhere, they might be separated from the existing distribution of a species by fundamentally unsuitable conditions that the species cannot cross. It is unrealistic for the climate-threatened golden bowerbird *Prionodura newtoniana* that is endemic to the mountains of Queensland to descend to lower elevations, spread across the hot lowlands, and colonise cooler areas further south in Australia [49]. If such species had been capable of establishing in, and spreading across, the intervening lower land, they would have already done so. A hundred years of climate warming is going to make the lowlands even less hospitable and their journeys harder, not easier.

The open question is 'how many climate-threatened species with small distributions could thrive if they were transported to appropriate locations elsewhere?' The answer is not known, but some historical introductions of species are relevant to the question. Rhododendron *Rhododendron ponticum* ssp. *baeticum* from the Iberian Peninsula (albeit with some introgression from other *Rhododendron* species) and Himalayan balsam *Impatiens glandulifera* are two of many examples of species that had narrow distributions and are now established and widespread plants in Britain [50–52]. They failed to colonise Britain in 10 000 years of warm Holocene climates, until deliberately moved by horticulturists during the past 250 years. The Iberian endemic rabbit *Oryctolagus cuniculus* is another example, in this case introduced nearer to a thousand years ago [53]. It is likely that there are many other southern European species that could be established further north, were they to be moved.

Attitudes to these species (considerable sums are spent on their control) would be entirely different had they colonised Britain naturally or been brought by early humans. Stands of the free-flowering rhododendron and balsam would be regarded as among the flowering glories of the British Isles and these communities would be prized, on a par with native bluebell woods. Rabbits are more 'acceptable' because of their earlier date of arrival; they provide food for birds of prey and other native carnivores, as well as help to maintain traditional grazing on species-rich meadows. Interestingly, *R. ponticum* was present in Ireland [54] and rabbits in England during previous interglacials [55]. There appears to be an element of lottery (biogeographic contingency) about which species 'make it' to northern Europe in a particular warm period, and where species survive in climatic refugia when they do not [54–56]. On the timescale of glacial cycles, there is nothing 'special' about species' current ranges. Hence, there is nothing 'special' about conserving species within their current distributions, in the context of climate change.

In general, most species on Earth are restricted to small geographic areas [57], and climate-change disproportionately threatens small-range species that occupy disappearing climates within centres of endemism [6,8,10,48]. Most of the other species that are threatened by climate change are likely to be species that have become endangered for other reasons, such that their surviving populations are now restricted to regions that will become climatically unsuitable. For climate-endangered species of both types, translocation might be the only realistic conservation option, other than consigning their genes to storage.

On this basis, I suggest that translocation represents one of the principal means of saving species from extinction from climate change; in conjunction with maintaining large areas of high-quality (low human impact) habitats [17,58].

High and low risk translocations and destinations

The problem is where to move these species without causing problems. Most historically translocated species have remained rare within recipient regions, adding to regional species lists without always eliminating native species; hence increasing regional richness [59]. Nonetheless, approximately 40% of the historically documented species-level extinctions attributed to specific causes have been associated with invasive species, such as mammalian predators introduced to islands and predatory fishes introduced to lakes [60]. Essentially all of these species-level extinctions have (i) occurred in island-like environments that contained concentrations of endemic species, such as lakes and true oceanic islands, or (ii) involved the translocation of species to different biogeographic regions, such as

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moving species between continents. Moving placental mammals to Australia and New Zealand or amphibian skin pathogens of out of Africa are cases in point [30,60,61]. These are not the types of translocation being advocated under assisted colonisation.

The concentration of so many species into centres of endemism means that most other regions are dominated by relatively widespread taxa. Although introduced species can cause changes to the distributions and abundances of indigenous species in these regions, they do not normally bring about species-level extinctions. To the best of my knowledge, no native species has been extirpated as a result of non-native species (other than humans) establishing in Britain. Some native British species have declined and become more localised [59,62], but not extirpated from the whole of Britain. The largest declines of indigenous species in Britain stem from long-distance translocations (e.g. introductions from North America), which would not normally be sanctioned under a deliberate assisted colonisation policy. Hybridisation between some native and introduced plant species has even generated several new, apparently self-perpetuating, species [63]. The establishment of a couple of thousand introduced species in Britain [62] has substantially increased regional species richness. Britain contains a geographically widespread subset of the European continental biota (it has been an island for only the past 8000 years or so), contains few endemic species, has its vegetation heavily modified by humans, and appears almost immune to extinctions from introduced species. Britain therefore represents an ideal destination for species displaced by climate change (Box 1). It is likely that suitable destinations elsewhere will also be characterised by a lack of endemic species, or will be regions where the endemics are restricted to particular types of environment that are resistant to the introduced species (e.g. endemics are associated with serpentine rocks; or with aquatic habitats when terrestrial species are introduced). I would argue that climate-endangered species should be welcomed in such areas, if they will help save the translocated species from extinction.

A substantial programme of work is needed to identify (i) the species and/or communities at greatest risk from climate change, and (ii) the suitable locations [assisted regional colonisation areas, (ARCS)] where the translocated species would be least likely to cause species-level extinctions. Given that most regions are not rich in endemics, there are many parts of the world available to consider as potential locations to receive species displaced by climate change. There is already progress in identifying which individual species and communities are at greatest risk from climate change (e.g. [6,8,10,48,64,65]). In the absence of formal projections, even simple assessments, such as ‘does a species live within 300 m of the top a mountain?’ or ‘is it restricted to cloud forest in a region of declining montane cloud cover?’ can provide preliminary risk assessments [65]. Picking the best translocation destinations is also difficult because many climate-threatened species currently have realised niches that are much smaller than their fundamental niches. Although introducing uncertainty, the latter is ‘positive’ from a conservation perspective as it implies that an exact climatic match between the current location and the destination might not be needed (the failure of some translocations can be accepted provided that they take place before a species is so rare that every remaining individual is ‘precious’).

There is a need to develop a long ‘shopping list’ of potential translocations and, where possible, put in place monitoring of extant populations to help identify when action is required. The later it is left, the harder and more expensive translocations will become.

Box 1. A British ARC area?

Britain is an ideal recipient location for translocated species. Approximately 2000 introduced species have already become established [62] without indigenous species being extirpated as a consequence. A British ARC would contribute to the conservation of globally threatened species. The following represent a few examples that could be considered for translocation. In each case, natural colonisation is highly improbable.

Pyrenean desman *Galemys pyrenaicus*
The Pyrenean desman is a distinct (monotypic genus) semi-aquatic insectivorous mammal that is restricted to streams in the Pyrenees/NW Iberia, where it is threatened by climate change [66]. Establishing populations in streams in western Britain might be feasible.

Iberian lynx *Lynx pardinus*
The Iberian lynx is the most endangered cat in the world and is restricted to the Iberian Peninsula. It is descended from lynx that lived more widely in Europe before the late Pleistocene arrival of the now-widespread Eurasian lynx, *Lynx lynx* [67]. Establishment of the Iberian lynx in Britain would represent a greater contribution to world conservation than re-introducing the Eurasian lynx. Rabbits, the main prey of Iberian lynx, are abundant in southern Britain.

Spanish imperial eagle *Aquila heliacea adalberti*
The Spanish imperial eagle is an extremely rare eagle that is endemic to Spain and Portugal. It is potentially threatened by climate change [68] and its main prey is also the rabbit.

Provence chalkhill blue *Polyommatus hispanus*
The Provence chalkhill blue butterfly is restricted to northern Spain, southern France and northern Italy. It is currently at serious risk of extinction from climate change and southern England is predicted to become climatically suitable [69]. The host plant of the butterfly already grows on calcareous grasslands in southern England.

de Prunner’s ringlet *Erebia triaria*
de Prunner’s ringlet is a butterfly that is endemic to southern European Mountains and one that is threatened by climate change. Projections suggest that England represents a considerable portion of its potential new range [69]. The larvae feed on grass species that are already common in Britain.

Iberian water beetles
Many of the 120 water beetle species endemic to the Iberian Peninsula are narrow endemics that occupy headwater streams in one or a few mountain ranges [70]. They are under threat from increased droughts.

Caucasian endemics
Many species are endemic to the Caucasus Mountains and to disjunct humid forests of the eastern Black Sea coast and southern Caspian. Major reductions in summer precipitation are projected for this region, threatening moisture-dependent species. For example, the Caucasian wingnut tree *Pterocarya fraxinifolia* is restricted to moist habitats in the Caucasus, Turkey and Iran. It grew wild in the British Isles in previous interglacials, and establishes in gardens today.

Acknowledgements

I thank many colleagues for sharing their thoughts on conservation in the context of climate change, and three anonymous referees for their comments on the article.

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